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Development of Terminal Buds in Pinyon Pine and Douglas-Fir Trees

by

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CHARLES L. DOUGLAS AND JAMES A. ERDMAN[1]

INTRODUCTION

Various scientific investigations recently have been conducted under the auspices of the Wetherill Mesa Project to learn more about the ecology of Mesa Verde and, particularly, to what extent ecological factors may have influenced the lives of the prehistoric Indians who once lived in this area.

This report presents the results of phenological observations undertaken in conjunction with, and as a supplement to, a study of the growth of conifers in Mesa Verde National Park. A method is presented for assigning developmental stages to the continuum of terminal bud extension and growth. The relationship of these stages to radial growth of the stem is discussed.

Mesa Verde is situated in the southwestern corner of Colorado, about 30 miles northeast of the Four Corners marker where Arizona, Colorado, New Mexico and Utah meet at a common boundary point. Mesa Verde National Park, well known for its cliff dwellings of prehistoric Pueblo Indians, occupies about one-third of the area of the Mesa Verde.

The northern escarpment of the Mesa Verde land mass towers nearly 2,000 feet above the surrounding Montezuma Valley. The Mesa Verde, named by early Spanish explorers, is a plateau that has been dissected by erosion until it resembles narrow, fingerlike mesas joined at their northern ends, but otherwise separated from each other by deep canyons. These fingerlike parts of the plateau are incorrectly called mesas, although common usage has firmly established the practice. The land mass is composed of interbedded strata of sandstones and shales, deposited by Cretaceous seas. The highest elevation in the park is 8,575 feet, at Park Point, on the northern rim of the plateau; from here the plateau slopes gently southward to an elevation of about 6,500 feet at the southern ends of the mesas. Drainage is southward into the Mancos River, which has cut a canyon, about 1,000 feet deep, that separates Mesa Verde from Johnson Mesa to the south (Fig. 1).

Soils on the mesa tops are predominantly wind-deposited loess, of varying depth. Soils in the canyons are for the most part alluvial in origin, and deep, well-drained alluvial terraces are common in the bottoms of larger canyons. The soils of the park have been studied recently by Orville A. Parsons of the

[1] Texas Memorial Museum, The University of Texas at Austin, and Fort Lewis State College, Durango, Colorado.

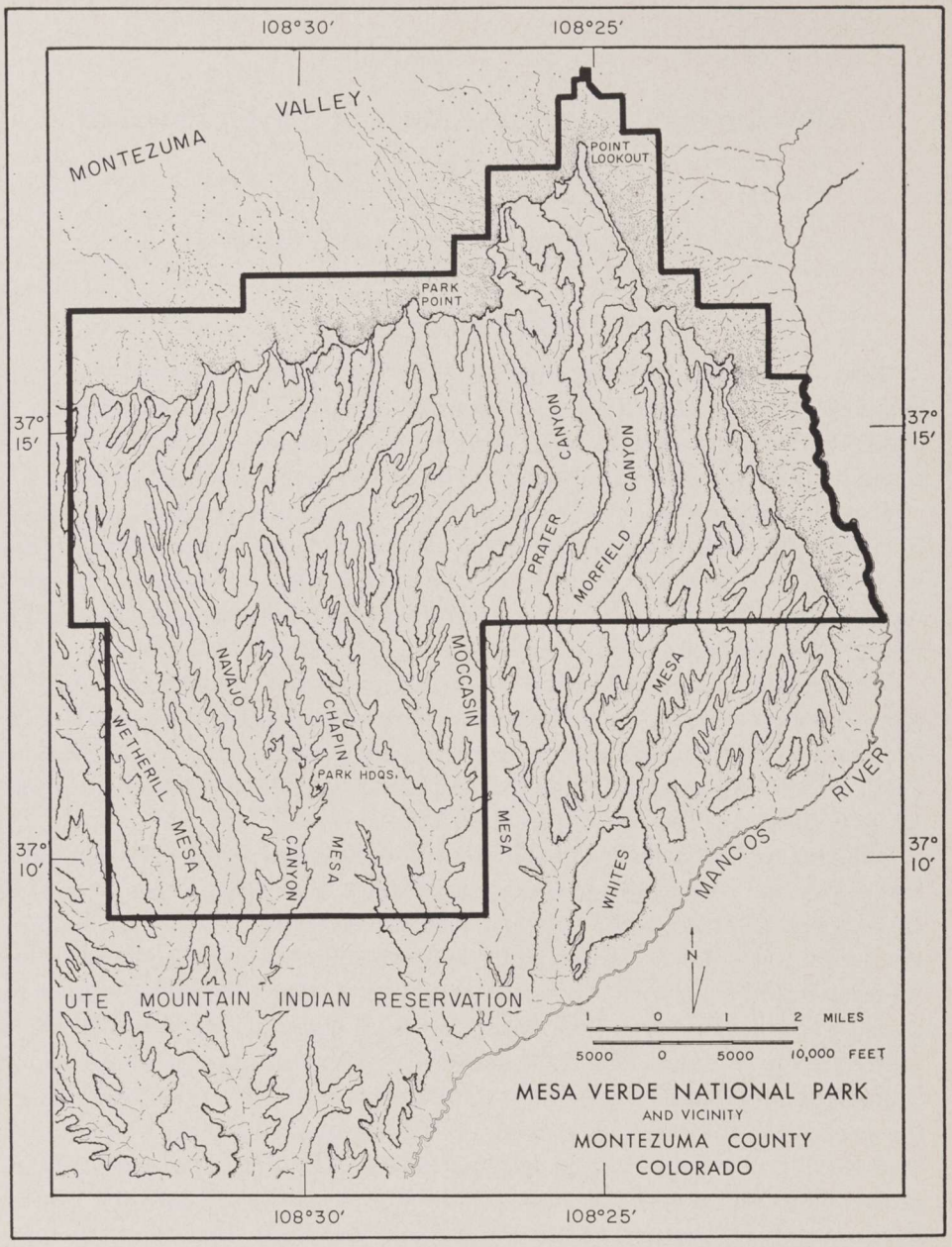


Figure 1. Map of Mesa Verde National Park and vicinity, showing locations of study areas for conifers. Pinyons were in stands on opposite talus slopes of Navajo Canyon, ¼ mi. W. of Park Headquarters and on the mesa, 1 mi. N. of Park Headquarters. Douglas-fir trees were in a stand in a secondary canyon, ¼ mi. NE of the Navajo Canyon sites.

Soil Conservation Service, and the loess of Mesa Verde has been analyzed by Arrhenius and Bonatti (1965).

The vegetation and fauna of the park are largely Upper Sonoran in affinity

(Anderson, 1961; Douglas, 1966). The climax vegetation is pinyon-juniper woodland, which extends throughout much of the Southwest. Pinyon pine, *Pinus edulis* Engelm., and Utah juniper, *Juniperus osteosperma* (Torr.) Little, cover most of the mesa tops and talus slopes. Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, occurs in stands along the northern escarpment of the park; at lower elevations this species frequently occurs on protected slopes in canyons. Ponderosa pine, *Pinus ponderosa* Dougl., is rare, and occurs throughout the park as small relict stands, or as isolated individuals. Gambel oak, *Quercus gambelii* Nutt., and mixed shrubs (*Amelanchier utahensis* Koehne, *Fendlera rupicola* A. Gray, and *Cercocarpos montanus* Raf.) are abundant in the shrub zone along the North Rim and on rocky slopes. (For more information about the park's vegetation see Welsh and Erdman, 1964; and Erdman, Douglas, and Marr, in press.)

The development of terminal buds was studied because of its important relationship to growth in the stem and branches of a tree. The studies of many investigators have shown the buds to be the first source of growth hormones (auxins) that promote cambial division in the spring.

Early investigators felt that in the spring increasing levels of moisture and temperature stimulated cambial activity (Brown, 1912, 1915). Priestley (1930) was among the first to recognize that the initiation and spread of cambial activity is linked to the apical meristem and that the stimulus travels basipetally. Priestley agreed with Brown (1912) that there is separate resumption of activity in the main axis and in the main branches of conifers, but stated that in either case the activity begins at the base of the buds. Wight (1933) disagreed with the concept of separate inception of growth in the trunk and branches and reported that activity in *Pinus sylvestris* L. starts simultaneously in all branch apices, only appearing to originate in the active upper branches. Fraser (1952) agreed with Priestley's report on basipetal movement of the stimulus, and reported that in white pine and other Canadian trees the cambial stimulus proceeds from the apex downward and from branch apices inward.

Dendrometer studies led Fraser (1952) to disagree with Priestley's concept that cambial activity in American trees is stopped by frost. Fraser's data indicate that summer growth is completed long before frost. The findings of Hess (1959) on studies of *Pinus ponderosa* are in agreement with those of Fraser, as are the findings of Fritts, *et al.* (1965) on studies of *Pinus edulis* and *Pseudotsuga menziesii.*

Snow's investigations (1933, 1935) introduced the concept of auxins as regulators of cambial stimulation. Snow concluded that normal cambial division is activated by the growth hormones produced in the leaves, which also promote cell extension.

Wareing (1951) hypothesized that there may be an auxin precursor in the cambium that is activated by the expanding buds. In studying differences between ring-porous and diffuse-porous trees, Wareing found that small

amounts of bud growth lead to stimulation of vessel development over large distances in ring-porous species. In diffuse-porous species, the cambial activity stimulated by the early development of the buds is very slight. This led to the suggestion that the pattern of cambial initiation in ring-porous species is due to a reserve of auxin precursor in the cambium. It has also been suggested that cambial activity in conifers, as in ring-porous hardwoods, is not exclusively dependent on hormones from the terminal buds (Brown and Cormack, 1937; Wareing, 1951; Kramer and Kozlowski, 1960). Pinyon pine and Douglas-fir may be similar to ring-porous angiosperms, since they both have well developed spring and summerwood.

Larson (1960) studied auxin gradients and cambial activity in *Pinus resinosa* Ait., and found a correlation between the cessation of growth of the shoot in length and the beginning of the production of summerwood. Summerwood production was found to progress from the base of the shoot to the tip as shoot growth slowed down. Cessation of shoot growth occurred under short-day photoperiods, and was accompanied by drastically reduced meristematic activity and a reduction of auxin synthesis. If the shoot apex was removed at this time, summerwood production was initiated just below the apex. Treatment of the decapitated stem tip with indole-acetic acid, however, produced large diameter springwood cells—even under short-day photoperiods. The continuation of long-day photoperiods at the end of the period of shoot elongation caused continued growth in length and continued production of springwood cells. Larson's study strongly suggests that differentiation of xylem is controlled, at least in part, by auxin.

In pinyon pine and Douglas-fir trees, the terminal bud that is formed in the autumn contains the embryonic stem and all of the embryonic needles that will form the following season's terminal growth. Some buds form only stem and needles, while others also produce staminate or ovulate cones. The rapid extension of terminal buds in the spring is due largely to expansion and elongation of cells formed in the preceding autumn.

It is a moot question whether the earliest phases of terminal extension should be termed growth or development. New materials undoubtedly are incorporated into the cytoplasm and into the elongating cell walls, and this could be considered as growth. On the other hand, because the cells were laid down in the preceding year, they could be considered as only undergoing maturation or development. In this report, development will be considered to occur first and to grade imperceptibly into growth. We cannot say precisely at what stage development of pre-existing cells terminates and new cellular division begins; therefore, we have used the term "development" in an all-inclusive sense.

Terminal bud development was followed in 29 pinyon pine trees, and in six Douglas-fir trees during the growing seasons of 1962 and 1963. The study trees were the same as those used by Fritts, *et al.* (1965) in their study of tree growth. Pinyon pines were studied at three sites. One site was on Chapin

Mesa at an elevation of 7,150 feet, one mile north of Park Headquarters. Two canyon sites were at elevations of 6,500 feet on northeast- and southwest-facing talus slopes in Navajo Canyon, about one-quarter of a mile west of Park Headquarters (Fig. 1). Douglas-fir trees were studied in a stand on the west-northwest-facing slope of a narrow secondary canyon draining into Navajo Canyon. This stand is at an elevation of 6,700 feet, about one-quarter of a mile northeast of the two pinyon pine sites (Fig. 1).

Phenological observations and servicing of growth instruments were carried out through the efforts of the authors and David G. Smith. During the second summer of the study, while we were occupied with other studies, Smith took over the phenological observations.

Instruments were read and serviced, and phenological observations were made at approximately weekly intervals throughout the growing seasons. A report resulting from the growth study contains an analysis of climatic factors influencing tree growth, and a model for paleoclimatic interpretation of tree rings from Mesa Verde (Fritts, *et al.*, 1965). Information from dendrograph records as well as anatomical data pertaining to radial growth of the stem have been condensed from the report mentioned above. To our knowledge, no previous attempts have been made to assign developmental stages to terminal extension and growth.

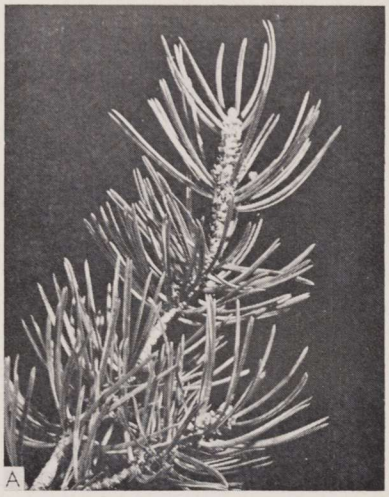
TERMINAL DEVELOPMENT IN PINYON PINE

The inception of each growing season becomes apparent when the terminal buds begin to swell. As swelling progresses, the overlapping bud scales part slightly from each other, or individual bud scales may split. In either case, the uncovering of previously unexposed portions of the bud scales causes the bud to be lighter in color. In pinyon pines such swelling of the buds occurs during the latter half of May and is accompanied by swelling of the cambium, and initiation of cambial activity in the stem.

The tissues of the buds develop rapidly and soon cannot be contained by the bud scales; consequently the scales are pushed aside as the bud elongates. Soon pollen cone primordia begin to mature, and become noticeable as small nodules on the sides of some buds. These primordia are apparent on some pinyon pine trees by mid-May, and by early June they are well developed on all trees. Ovulate cones become apparent on other branches at this time. The appearance of pollen cone primordia is accompanied by differentiation of newly formed phloem in the stem of the tree.

As the pollen cones ripen, the microspores mature into pollen grains. The microsporangia containing the pollen grains split about mid-June and the slightest breeze or other disturbance of the branches releases clouds of sulfur-colored pollen. Immediately after the pollen is shed, more regular growth becomes apparent in the stem.

As mentioned earlier, the phloem cells are the first to be formed. Xylem is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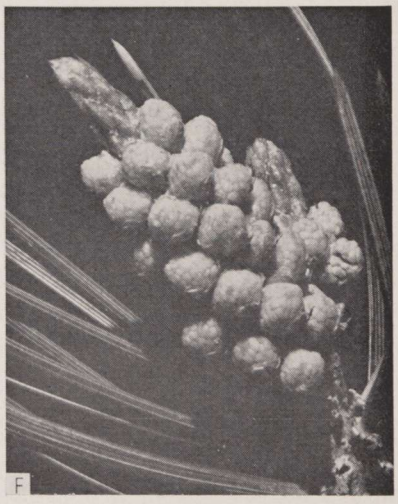
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produced from about the last week in May until about the first week in August. The yearly increment of xylem is composed of earlywood and latewood, the cells of which are first laid down and then lignified. By August 9, 1962, all but the last row of latewood cells were lignified (Fritts, *et al.*, 1965).

The cambium returns to a resting state after the yearly increment of xylem is formed, and overwinters as a narrow band of cambial initials (Douglas, 1961). This resting state was reached in early August, 1962, by pinyon pines.

Needle primordia present in the bud begin their major extension after pollen is shed. Each pair of new needles is covered by a fascicular sheath; the needles extend rapidly, break through the sheath, and separate from each other. The needles grow from a basal meristem. New needles extend from late July into mid-August on most trees, although needles continue to extend on a few trees until the last week of August (Fritts, *et al.*, 1965). The major internodal extension of the new stem is largely completed by the time pollen is shed.

Terminal development was followed in buds and in new growth (stem and needles) on lateral branches of the two species of conifers. At first, the development of buds was described in detail for each tree, but this consumed too much time, and thus it was necessary to assign arbitrary stages to the development. The stage of bud development most prevalent over the entire tree was recorded in each case. Terminal ends of branches were removed periodically from other trees in the study areas, and photographs were made of each stage of bud development.

Five stages of bud development were subsequently defined for pinyon pine; the distinguishing characteristics of each stage are summarized as follows:

STAGE I: Preceded by a quiescent terminal bud. This stage characterized by swelling of terminal bud, followed by separation of overlapping bud scales, or splitting of individual scales (Figs. 2a and 2b). Late April and early May. No cambial activity.

STAGE II: Extension or elongation of the terminal bud. Bud shows no pronounced constriction, or neck, at its proximal end (Figs. 2c and 2d). Early to late May. Swelling and initiation of cambial activity occurred in latter half of May, 1962 (about May 14–21).

STAGE III: Pollen cone primordia present; bud elongates and pollen cone primordia swell until they reach development shown in Figs. 2e and 2f. Terminal buds without pollen cones have prominent neck at proximal end, where new branch is forming (Fig. 3a). Mid-May to first half of June. Phloem cells differentiating; first xylem cells laid down during last week in May.

STAGE IV: Release of pollen by pollen cones; all pollen shed by end of stage IV

Figure 2 (a-f). Terminal buds of pinyon pine, showing general and close-up views of various stages of development. (a-b) Stage I. Swelling of terminal buds and separation of bud scales. (c-d) Stage II. Extension of terminal bud. (e-f) Stage III. Pollen cone primordia present.

(Fig. 3b). First half of June; stage terminated by June 15, 1962. Release of pollen precedes more regular rate of xylem production.

STAGE V: Needles emerge from fascicular sheaths and continue to extend (Fig. 3c). Late July to mid-August. Xylem formation terminated in about the first week of August. Cambium quiescent by August 9, 1962.

TERMINAL DEVELOPMENT IN DOUGLAS-FIR

Terminal buds of Douglas-fir trees follow a sequence of development similar to that in buds of pinyon pine, although there are some fundamental differences between the two species. In Douglas-fir the terminal development is rapid; swelling of the buds begins in about the last week of April. Initially

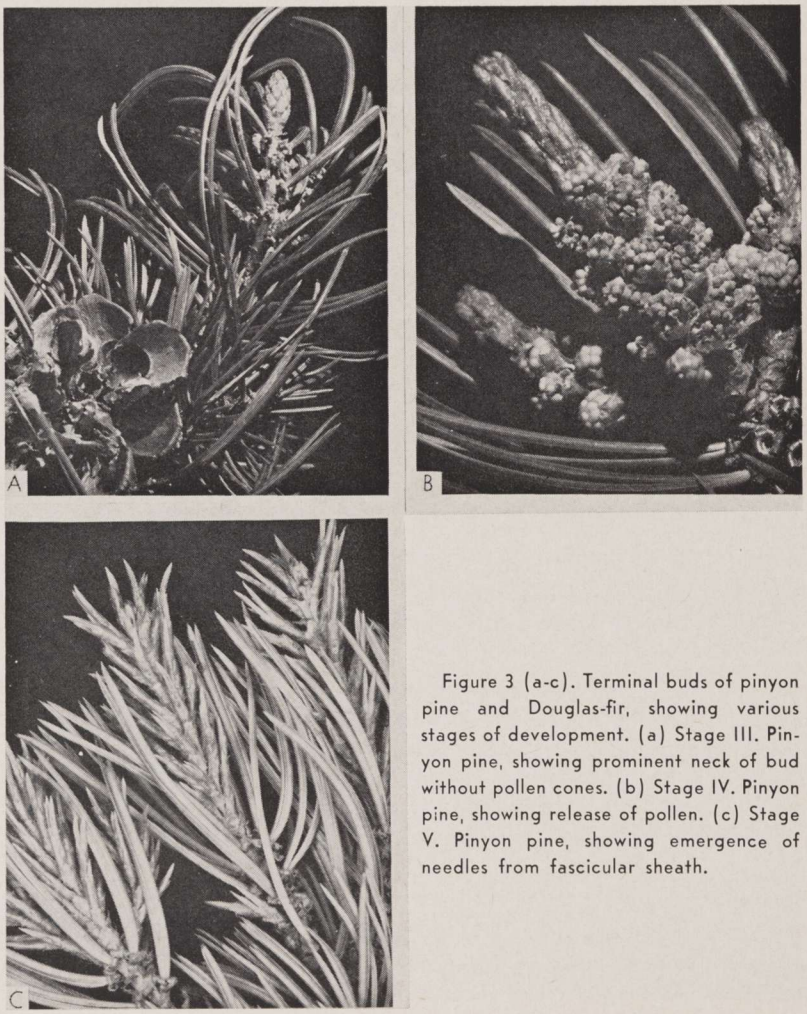


Figure 3 (a-c). Terminal buds of pinyon pine and Douglas-fir, showing various stages of development. (a) Stage III. Pinyon pine, showing prominent neck of bud without pollen cones. (b) Stage IV. Pinyon pine, showing release of pollen. (c) Stage V. Pinyon pine, showing emergence of needles from fascicular sheath.

the dormant bud is maroon, but progressive expansion of the bud and separation of the bud scales causes the color to change first to yellowish and then to ivory.

The bud elongates rapidly, but to a lesser degree than in pinyon pines. The expanded bud is first composed of a cluster of embryonic needles. A thin covering, apparently composed of several scales, surrounds the entire cluster of needles; individual needles do not have sheaths. Soon the needles erupt through their covering of scales. At this time the needles appear as a brush-like cluster; after they emerge from their covering, they separate by bending away from each other. As the internode elongates, the needles are carried away from each other to form their more typical spacing about the branch. The needles do not have basal meristems, and complete their maturation by about the first week in June. Most of the internodal extension of the shoot takes place within one week.

Pollen is shed in late May, while major radial increase of the trunk is in progress. Seeds are dropped from the cones in autumn.

Radial growth of the stem becomes apparent at breast height within about 12 days after swelling of the buds on lateral branches. The major increase in diameter of the trunk occurs during the month of May. Dendrograph records indicate that some growth continues into the first part of June, but all growth terminates by the middle of the month (Fritts, *et al.*, 1965, Fig. 3).

Four stages were assigned to the terminal development of Douglas-fir; the stages are summarized as follows:

STAGE I: Preceded by a quiescent terminal bud. Swelling of terminal bud and separation of overlapping bud scales. Color of bud changes from maroon to yellowish (Figs. 4a and 4b). Last week of April.

STAGE II: Elongation of terminal bud. Color of bud changes from yellowish to ivory (Figs. 4c and 4d). Last week of April.

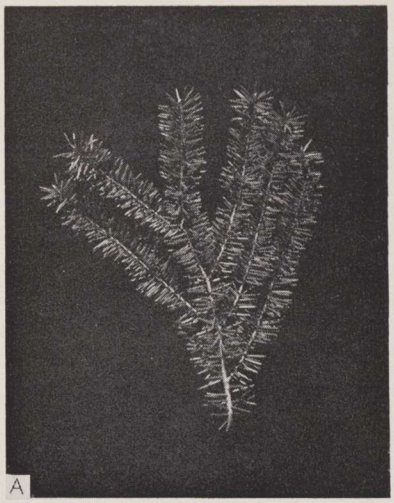
STAGE III: Eruption of needles through bud-scale sheath. Last week of April to first week of May (Figs. 4e and 4f). Radial growth started on about 5 May 1962.

STAGE IV: Stem elongation and formation of new terminal bud. Tip of stem is red; color of quiescent bud is maroon (Fig. 5). First part of May to early June. Radial growth terminated during last week of May 1962. All new stem growth mature by end of first week in June.

Anatomical information is not yet available for Douglas-fir trees in Mesa Verde, although studies are in progress by Marvin Stokes, Laboratory of Tree-Ring Research, University of Arizona.

DISCUSSION

Some differences in terminal extension are readily apparent between the two species of conifers. Terminal development in Douglas-fir is greatly accelerated in comparison to that in pinyon pine. The reduced leaves of the two species are not morphologically comparable, for the pine needles represent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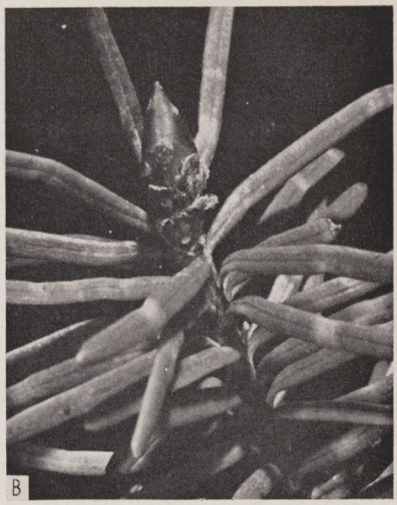
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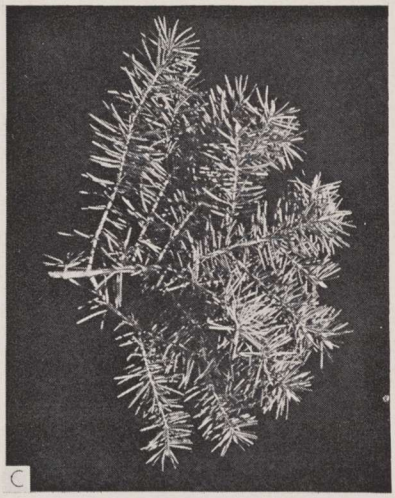
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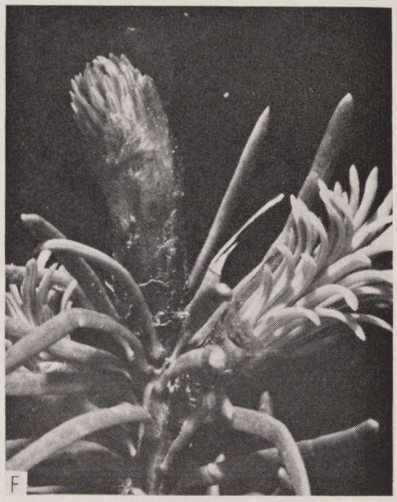
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Figure 5. Terminal bud of Douglas-fir, showing new bud and mature terminal growth of the season.

leaves on a lateral bud, whereas the leaves of Douglas-fir are primary leaves of the main branch (Doak, 1931). In pinyon pines the major extension of the needles begins after pollen is shed and continues for several weeks after the cessation of cambial activity. In Douglas-fir, pollen is shed while the needles are extending. Extension of the needles in Douglas-fir trees begins concurrently with the initiation of radial growth, and terminates several weeks before radial growth stops. In Douglas-fir, pollen is shed while major radial increase of the stem is in progress, but in pinyon pines, pollen is shed prior to major stem growth.

Radial growth in Douglas-fir begins in early May and ends in late May or early June, whereas radial growth in pinyon pines begins in late May or early June and ends between late July and mid-August. The dates of occurrence given for each stage of terminal development should be considered as approximations. The precise time bud development begins and terminates is, of course, dependent upon climatic and microenvironmental variables, as well as upon the idiosyncracies of individual trees. For example, the growing season of 1963 was wetter than that of 1962, and in 1963 both species began growth about one week earlier, and terminated growth about one week later, than in 1962.

Douglas-fir is a representative of Transition zone vegetation in the park, and grows there only in relatively cool, moist microenvironments. In Mesa Verde, Douglas-fir trees complete their seasonal growth prior to the hottest, driest part of the summer. In this species the seeds ripen in the same year in which pollination takes place. Apparently this species is adapted for rapid

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Figure 4 (a-f). Terminal buds of Douglas-fir, showing general and close-up views of various stages of development. (a-b) Stage I. Swelling of bud and separation of overlapping bud scales. (c-d) Stage II. Elongation of bud. (e-f) Stage III. Eruption of needles through sheath of bud scales.

growth and rapid production of seeds, perhaps so that it can survive in montane regions where there are short growing seasons.

Pinyon pine is adapted to the more arid climatic conditions that prevail in the Upper Sonoran life zone, and consequently this species utilizes more of the summer for growth than does Douglas-fir. The seeds ripen and are dropped in the year following that in which pollination takes place.

It would be interesting to know how much earlier the apical buds begin developing than do the lateral buds. Apical buds of both species undoubtedly reach each developmental stage somewhat earlier than do buds on lateral branches. The inspection of apical buds was not practicable under the existing field conditions, whereas inspection of buds on lateral branches was accomplished easily. Cambial initiation was evident, at breast height, in the stems of pinyon pines several weeks after buds on lateral branches began developing. Dendrograph records indicate that growth was apparent in Douglas-fir trees about 12 days after expansion of the buds (Fritts, *et al.*, 1965, Fig. 3). Lateral buds would be expected to contribute auxins primarily to the branches, but little to the stem. It is probable that the development of lateral buds may lag as much as a week behind that of the apical buds.

Auxins produced by the meristems of extending needles are known to control latewood formation in *Pinus resinosa* Ait. (Larson, 1962). The data suggest that this probably is the case in pinyon pine, but not in Douglas-fir. If maturing needles provide auxins for latewood production, one would expect needle extension during, and possibly after, the time of latewood formation. Needle extension in pinyons continued for several weeks after cambial activity had stopped, whereas needle extension in Douglas-fir began at the start of radial growth and was largely completed by as much as several weeks before cessation of cambial activity (Fritts, *et al.*, 1965). This poor correlation between needle extension and production of latewood probably is due to the absence of a basal meristem in needles of Douglas-fir, and a consequent lack of auxin production by leaves of this species. Latewood formation in Douglas-fir probably is controlled more by the apical meristem than by the needles.

Fritts, *et al.*, (1965) suggest that needle lengths on lateral branches may reflect climatic conditions during the growing season in which they were formed, whereas needles on apical branches appear to reflect climatic conditions that preceded the growing season.

It has been shown that the amount of xylem produced each year by both pinyon pines and Douglas-fir is affected more by climatic conditions during the previous growing season and prior to the current growing season, rather than conditions during the current growing season (Fritts, *et al.*, 1965).

In an earlier study, it was shown that severed terminal leaders of white pine broke dormancy and exhibited rapid terminal extension when they were brought into the laboratory, supplied with water, and placed under a 24-hour photoperiod (Douglas, 1961). It was found that the cambium of such de-

tached leaders produced a complete band of new springwood cells around its circumference. When terminal leaders were girdled, by removing a band of bark and cambium a few centimeters below the terminal bud, a complete band of springwood was formed above the girdle, but only an incomplete band was formed below the girdle. Apparently small lateral buds on branches below the girdle contributed auxins for the formation of the incomplete bands of springwood. The evidence indicates that considerable development and growth can take place in terminal leaders, even when they are isolated from the rest of the tree. Food stores formed in the tree during the previous growing season have thus been shown to have the potential for providing nutrients, and probably building materials, for terminal development and growth the following spring. It is not known whether such stored foods are used for this purpose under normal conditions. It also is possible that photosynthetic activity in older needles may produce enough carbohydrates during the early phases of terminal extension to provide any necessary building materials. The precise climatic, nutrient and physiological combinations responsible for initiating terminal extension in the spring and terminating it in the autumn are poorly understood.

These findings and those data mentioned earlier would tend to support the hypothesis that in the spring the materials necessary for terminal extension, and at least the early stages of cambial division, depend heavily upon food stores formed by the tree during the previous growing season. Perhaps the tree first utilizes stored foods and water during the more critical stages of growth, then replenishes these supplies as climatic conditions become more favorable for photosynthesis and absorption of nutrients. If this is the case, a poor growing season would be reflected in a narrow increment of xylem laid down during the next growing season. And conversely, a good growing season would be reflected by a wider increment of xylem in the growth of the following season. The preceding discussion indicates that there is such an interrelationship; therefore the hypothesis appears to be consistent with the data. This is undoubtedly an oversimplification, but perhaps future studies will clarify the complex interactions that take place within conifers during successive growing seasons. Further study of terminal development probably will help clarify the interrelationships between production of hormones in the buds and the formation of seasonal increments of xylem and phloem in the stem.

ACKNOWLEDGMENTS

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